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The life-cycle of *Diplostomum spathaceum* (Rud. 1819) in brackish waters of the Baltic Sea

Cykl rozwojowy *Diplostomum spathaceum* (Rud. 1819) w wodach słonawych Morza Bałtyckiego

The aim of the present study is to examine the possibility of the closing of the *Diplostomum spathaceum* (Rudolphi 1819) life-cycle within the brackish environment of the Baltic Sea inshore waters and to find out whether this occurs in the same way as in fresh water in which it was being hitherto studied.

The *Diplostomum spathaceum* (Rud.) development was examined and described by many scientists, such as Braun 1894, Blochmann 1910, Fuhrmann 1916, and Szidat 1924, while the morphology of its particular stages of life was described by the authors already mentioned and by Komiya 1938, Dubois 1929, Wesenberg-Lund 1934 and others; the pathogeny was described by Markevič 1934, 1951, Baylis 1939, Kozicka 1955. The life-cycle of this parasite as well as a relatively long list of its hosts was established as a result of this research work.

The first hosts of the sporocyst mentioned in the literature were exclusively the snails of the family *Lymnaeidae*, belonging to a previously extensive genus *Lymnaea*, namely: *Lymnaea stagnalis* L., *Radix ovata* (Drap.,), *Radix auricularia* (L.) and *Stagnicola palustris* (O.F.M.).

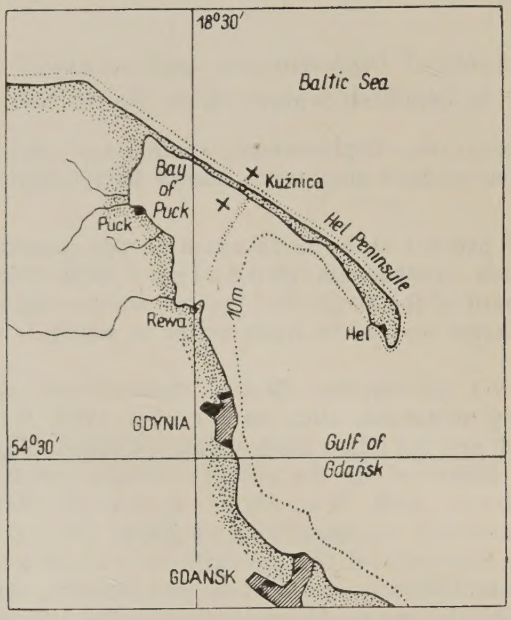
The fresh-water fishes of Europe, Asia and North America, in all about 60 mentioned species (first of all *Cypryniformes*) are the hosts of the metacercaria. Markevič 1951 wrote that *D. spathaceum* (Rud.) metacercaria were noticed in the eyes of fish in the Aral, Caspian, the Black, White and the Baltic Seas.

Piscatory birds are the hosts of the mature forms: *Larus argentatus* Pont. *L. argentatus cachinnaus* Pall. = *Larus michahellosi* Bruch, *L. canus* L., *L. fuscus* L., *L. glaucus* Brümn, *L. leucopterus* Fab., *L. marinus* L., *L. ridibundus* L., *Rissa tridactyla* L., *Stercorarius parasiticus* L., *Alca torda* L., *Morus bassanus* L., *Sterna hirundo* L.

The above list is indicative of an insignificant degree of specificity of the parasite at the different stages of its development. The specificity is the less significant at the metacercaria stage while it is the highest at the sporocyst and the cercaria stages.

Specification of environment

The region where the examinations were being carried out was limited to the Bay of Puck itself near Kuźnica — see enclosed map. It is separated from the deeps by the sand-bank Rewa — Kuźnica and is very shallow with an insignificant salt content (according to the Sea Fishery Institute, the water of the Hel and the Bay of Puck contained 0.6 — 0.7 per cent. of salt in 1957 and 1958). The fauna occurring here (particularly the molluscs and fish) represent a mixture of maritime and fresh water species. *Theodoxus fluviatilis* L.,



Radix ovata var. *baltica* Nilss. and *Esox lucius* L., *Gasterosteus aculeatus* L., and *Pungitius pungitius* L., belong to the fresh-water species occurring here. They become dwarfish under the sea conditions. So, for instances, the snail *Radix ovata* L. measuring 20 — 24 mm. in hight and 14 — 15 mm. in width or 25 — 35 mm. and 25 — 35 mm., respectively, attains only 14 mm. in lenght and 8 mm. in width as *R. ovata baltica* Nilss. in the brackish condition of sea. But on the other hand a decrease of the dimensions of the sea molluscs such as *Mytilus edulis* L. or *Cardium edule* L. may also be observed.

The material for the present study was collected from an area of the shallow sand bottom, according to the classification by Demel 1934 — 35. This shallow area is approximately 3 metres deep, overgrown with algae, especially with *Chara baltica* and chlorophyta as well as with *Ulva* sp. sp. The following molluscs settled at the shallow bottom: *Radix ovata* var. *baltica* Nilss, *Hydrobia ulvae* Penn., *Hydrobia ventrosa* Mont., *Hydrobia jenkinsi* Smith, *Cardium edule* L., *Theodoxus fluviatilis* L., *Mya arenaria* L., *Mytilus edulis* L. Among crustaceans there are *Palaemon adspersus* R., *Gam-*

marus sp. sp., *Idotea baltica* Pall., *Idotea viridis*, *Mysis mixta* Lill., *Neomysis vulgaris* Thomps., *Mysis aculeata* Lov. Fish fauna is represented by *Gobius niger* L., *G. minutus* L., *G. minutus* var. *microps* Kr., *Gasterosteus aculeatus* L., *Pungitius pungitius* (L.), *Esox lucius* L., *Siphonostoma typhle* L., *Nerophis ophidion* L., *Anguilla anguilla* L., *Pleuronectes flesus* L. The rich avifauna of this brackish zone is represented by many birds of the *Laridae* family; first of all by *Larus ridibundus* L.

The intensity of invasion of the hosts

The material for the present study was collected in the summer months: July and August 1959. In order to find out whether the process of the entire life-cycle of *D. spathaceum* (Rud.) occurred in the environment examined, the hosts of the particular developmental stages were searched for among the snails, birds and fishes. For this purpose the following were examined: the livers of the snails, the eye-lenses of the fishes and the intestines of the birds of the *Laridae* family. The following was established as a result of these examinations:

The cercaria developed only in *Radix ovata* var. *batlica* Nilss., in the area examined, while they never occured in *Hydrobia ulvae* Penn., *Hydrobia ventrosa* Mont., *H. jenkinsi* Sm., *Cardium edule* L., *Theodoxus fluviatilis* L., *Mya arenaria* L., *Mytilus edulis* L. The extent of the *R. ovata* var. *baltica* Nilss. invasion was relatively significant as 60 snails out of 103 examined (i. e., about 60 per cent.) were invaded.

Metacercariae were found in six species of fish mentioned in Table I. It may be seen that the extent of invasion varied with the fish species.

Table I

Extent of invasion of fishes with D. spathaceum metacercariae

Fish species	No. of fishes	
	examined	invaded
Gobius minutus L. +		
G.minutus var. microps Kr.	49	29
Gobius niger L.	15	6
Siphonostoma typhle L.	14	7
Nerophis ophidion L.	12	5
Esox lucius L.	5	2
Gasterosteus aculeatus L.	10	1
Anguilla anguilla L.	15	-
Together	120	51

The highest extent of invasion was confirmed in *Gobius minutus* L. and *G. minutus* var. *microps* Kr. while the *Gasterosteus aculeatus* L. as well as the *Anguilla anguilla* L. were practically not infected at all. It should be pointed out that the present authoress did not find any metacercaria of

D. spathaceum in fish (first of all in *Gobius minutus* L.) from the sea beyond the Hel Peninsula. This could be easily explained by the absence of the *Radix ovata* var. *baltica* Nilss. there.

The mature forms of *D. spathaceum* (Rud.) were found only in *Larus ridibundus* L. The intensity of the invasion was rather high: 229, 362 and 371 trematodes having been found in three old sea-gulls examined and 15 in one *Larus ridibundus* juvenalis.

Life-cycle stages in natural invasion

A. The sporocyst

The sporocysts are long, filiform, light gray in colour, rather immobile, filling up the liver of the snail almost entirely. Their size varies within the range of 330 to 3400 μ. They are filled with cercariae at different developmental stages.

B. The cercaria

The cercaria body is very expansible; the tail, when expanded to its utmost length, exceeds that of the body, the bifurcated branches are longer than the stem of the tail itself (Fig. 1). The entire body is covered with rows of very small spines, 10 to 12 such rows of densely arranged spines being disposed on the front end of the body. A pyriform anterior organ is situated in the front end of the body. A part of the former, covered with spines, can be drawn inside. The ventral sucker is situated slightly caudally off the middle of the body, provided with two crowns of spines. Four large coarse-grained penetration glands with vesicular nuclei are situated behind the ventral sucker; the two anterior ones are arranged behind each other while the posterior ones are arranged side by side. Sinuous efferent ducts run from the glands and open near the mouth opening. The tail is muscular and is covered with long chaetae, with the excretory duct inside of it; caudal bodies are concentrated around the duct. The dimensions of the cercaria from the brackish environment are the same as in the fresh water ones (see Table II).

Table II

The dimensions of cercariae of D. spathaceum (R u d.) - in microns

	Szidat 1924	Dubois 1929		Wesenberg Lund 1934	The own measurem.
Body	162-198 × 36-43	stretched 225-270 × 30-40	contract. 90-150 × 60-80	265 × 85	165-270 × 60
Tail-trunk	198	180-225 × 27-34		240 × 40	180 × 21
Furca	198	180-250 × 16-18		220	195
Anterior organ		40 × 25			54 × 39
Pharynx		12 - 14			
Ventral sucker	28	25 - 31		35	

The digestive system. From the mouth there run a praepharynx, a muscular pharynx, and an oesophagus bifurcating before the ventral sucker. Ramifications of the intestine encircle the ventral sucker and run up almost to the excretory bladder slightly parting to the sides.

The excretory system: The excretory vesicle, more or less rectangular in shape, is situated at the back of the body. Two main channels run from it along the both sides towards the front end dividing into the frontal and the caudal collecting channels at the level of the ventral sucker. The caudal

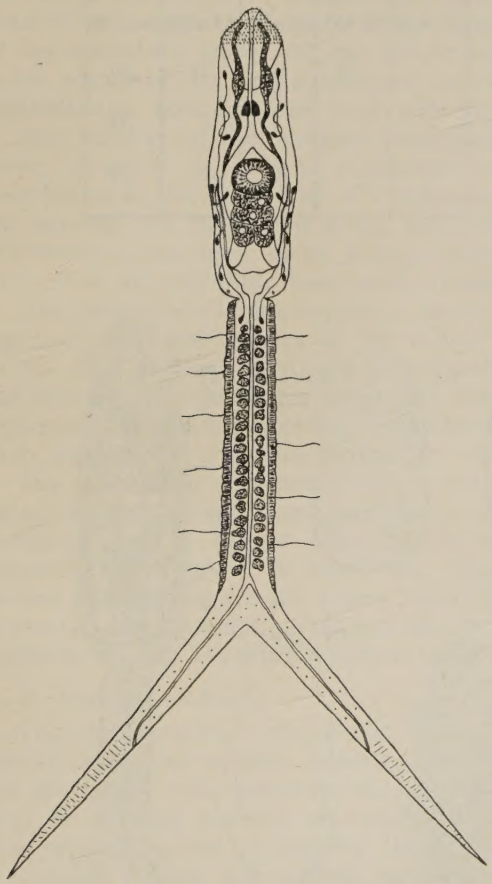


Fig. 1. *Diplostomum spathaceum* (R u d.) — cercaria

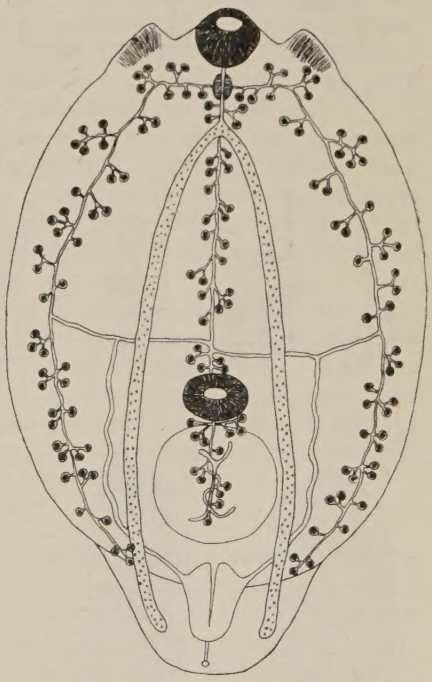


Fig. 2. *Diplostomum spathaceum* (R u d.) — metacercaria from *Gobius* — infravital

excretory channel runs backwards from the excretory vesicle along the whole length of the tail. Here, it separates into two branches running from the bifurcations and goes out in the middle of the inner edge of the latter. Capillaries from three flame cells lead into the frontal collecting channel while those from six such cells, one of them being situated in the tail, lead into the caudal collective channel. Fig. 1 ilustrates the layout of the flame

Table III

Dimensions of the succesive stages of the development of cercaria of D. spathaceum - Stages as in fig.3

	a	b	c	d	e	f	g	h	i
Body	60 × 36	69 × 30	61 × 34	105 × 63	114 × 63	66 × 57	93 × 51	114 × 45	168 × 51
Tail-trunk					57 × 45	75 × 55	36 × 30	57 × 24	84 × 24
Furca						18	18	33	90
Anterior organ									45
Ventral sucker							15		30

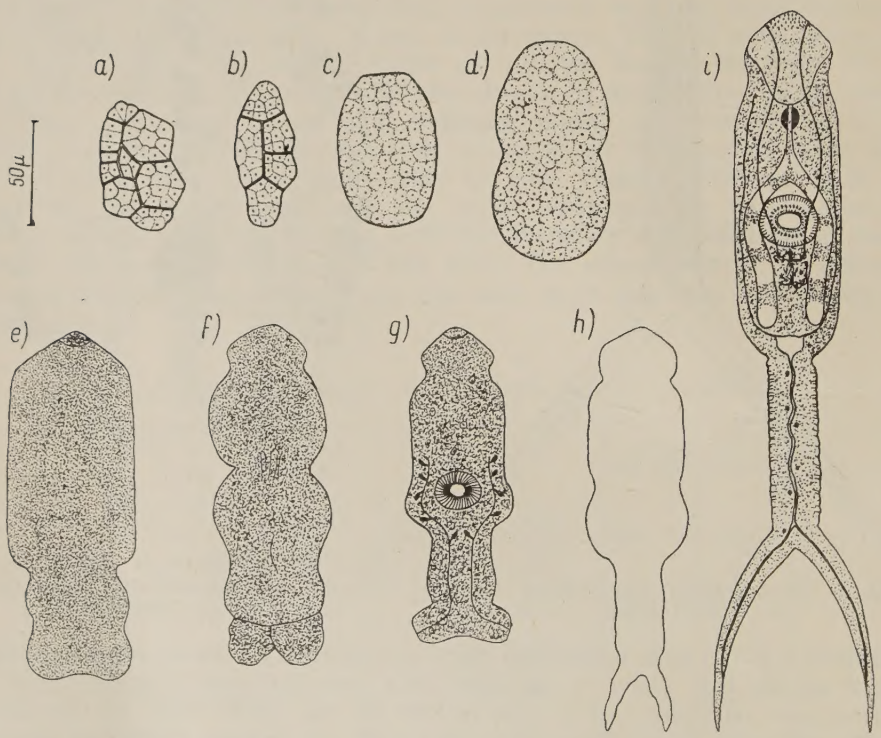


Fig. 3. The *D. spathaceum* (Rud.) cercaria development within the sporocyst from *Radix ovata* var. *baltica* Nilss.

cells. Thus, the formula of the excretory system observed by the present authoress was as follows: $2\times\{(3)+[5+(1)]\} = 18$.

Taking into consideration the Sewell's 1930 conclusion it seems that the flame cell N° III in IIIa and in IIIb and the cell N° IV in IV′ and IVa″, and in IVb′ and IVb″ was the only divided in this case. Then, the flame formula could read thus: the flame cells $2+\{(Ia + Ib + II) + [IIIa + IIIb + IVa' + IVa'' + IVb' + (IVb'')]\}$.

Dubois 1929 and Komiya 1938 gave the following formula for the excretory system of *D. spathaceum* (Rud.): $2\times[(3)+(3+(2))] = 16$, i. e., less than in the present authoress' observation. It is possible that the development of the excretory system of the cercaria examined by the present writer was more advanced for the subsequent transformation of the cercaria into the metacercaria goes hand in hand with an increase of the flame cells number.

The vitality of the cercaria examined was very high, and many of them were normally active and exhibited normal appearance after staying for four hours in the bay water (0.7 per cent. salt content) under the cover glass. On leaving the snail and going into water, the cercariae perform vertical movements, and very often remain suspended in a characteristic way with their fork up and their body bent almost perpendicularly to the tail.

The production of the cercariae bears a periodical character, and decreases together with the vitality of the snails. The present authoress noticed that, in the Bay of Puck during a rather windy period (6 to 7 m/sec) and with the morning temperatures markedly lower than the midday ones (13 C° of difference), the number of the cercariae in the snails was considerably smaller than during the preceding somewhat warmer periods.

On examining the cercaria in conditions of natural invasion, their development in the sporocyst had been traced back up to the stage of complete formation, ready to get out. This is represented in Fig. 3 a — i, and the dimensions are given in Table III. Only in 3g, the present authoress succeeded in marking off the flame cells. Komiya 1938 has published similar drawings and description of the development of the cercaria very precisely marking off the excretory channels and the flame cells.

C. The metacercaria

The metacercaria body is flat, wide, transparent, slightly concave on the ventral side and convex dorsally, covered with a smooth cuticle. A small and relatively wide appendix may be seen in the caudal part of older forms (Fig. 2). Lateral suckers are situated at both sides of the mouth opening. The ventral sucker is slightly larger than the oral one. A holdfast organ is situated behind the ventral sucker, twice the size of the latter. A short praepharynx runs from the buccal sucker continued by an obvious muscular pharynx, a short oesophagus, and caeca running down to the end of the body; the caeca are filled with a fine granular substance which is suggestive of food intake by the metacercaria.

Metacercaria has a markedly developed secondary excretory system. The body is filled with excretory corpuscles which considerably hamper the observations of the primary protonephridial excretory system. The excretory V-shaped vesicle is situated in the appendix at the end of the body. Two

lateral ducts lead from it frontally to the level of the front edge of the ventral sucker or even a little farther. At this point, they separate into two collecting ducts: the frontal and the caudal one. The caudal duct is situated between the main duct and the wall of the body, and reaches up to the region of the excretory vesicle. The frontal duct reaches up to the pharynx and, here, joins the contralateral frontal duct, henceforth running as a single duct along the middle of the body up to the holdfast organ to join with the lateral ramifications by means of a transversal commissure, before reaching the ventral sucker. Small ordinary or bifurcating ducts endig in calcareous bodies branch off these ducts (except for the main ones and the commissure). The dimensions of the metacercaria are given in Table IV.

D. Mature form

Two-segmented body (Fig. 4). Lobular front segment, very mobile, varying in shape. The praepharynx, the short muscular oesophagus and the intestinal

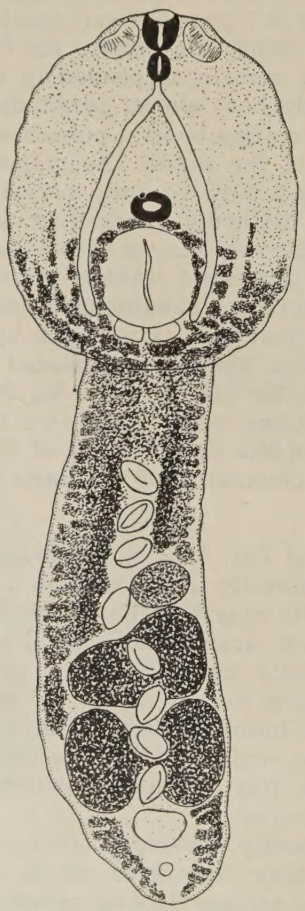


Fig. 4. A mature form of *D. spathaceum* (Rud.) from *Larus ridibundus* L.

Table IV

The dimensions of metacercariae of D. spathaceum (R u d.) in microns

	Komiya 1938 - fixed material	Own measurements -living material
Body	± 400 × ± 305	425-765 × 255-391
Oral sucker	± 51 × 58	± 51
Pharynx	± 21 × 38	-
Ventral sucker	± 44 × 51	51-54
Holdfast organ	-	68-105 × 68-180

Table V

Dimensions of the adult form of Diplostomum spathaceum (R u d.)- in microns

	Krause	Dubois 1939	Cichowlas
Anterior segment	600-1360 × 360-690	640-1800 × 270-960	731-1003 × 510-935
Posterior segment	770-2100 × 230-710	520-3220 × 210-750	850-1105 × 306-442
Oral sucker	54-94 × 54-99	40-100 × 48-104	68-75 × ± 51
Pharynx	41-81 × 36-72	48-91 × 26-75	-
Ventral sucker	54-110 × 59-140	48-101 × 48-130	± 60 × ± 96
Holdfast organ	220-410 × 77-130	125-450 × 90-432	119-165 × ± 119
Ovarium	77-130 × 100-170	50-205 × 70-235	± 102 × ± 170
Anterior testis	170-340 × 280-520	95-460 × 130-560	± 323 × ±459
Posterior testis	210-400 × 320-590	90-485 × 190-650	±306 ×±435
Egg	± 108 × ± 63	84-115 × 52-76	85-99 × ±40

branches bifurcating directly after the oesophagus run from the buccal suckers. The lateral glandular suckers are situated at both sides of the buccal one. A small ventral sucker is situated in the middle of the segment; not far off the former, behind it, the holdfast organ may be seen; its size may reach as much as 1/3 of the frontal segment width. The trunks of the excretory system run along the intestinal branches.

The caudal segment twice as long as the frontal one, narrow at the front and widening towards the end like a flask, is almost entirely filled up with the genital organs. Vitellary glands stretch along the both sides of the whole segment penetrating into the frontal segment, and extend beyond the holdfast organ. The frontally situated ovary ajoins the elongated testis; the other testis is bilobar with the bursa copulatrix following. The outlet of the short hermaphroditic duct is situated at the depth of the bursa copulatrix. The uterus is elongated in shape.

All these characteristics are in accordance with the features confirmed by Dubois 1929. The dimensions are compared in Table V. It can be seen from that Table that the *D. spathaceum* (Rud.) from the sea birds do not differ in dimensions from those of the inland birds.

Attempts at infestation

Experimental fish infestation was carried out in order to trace back the complicated process of the cercaria transformation into the metacercaria. Fish infestation with the *D. spathaceum* (Rud.) cercaria was carried on four occasions. *Gobius minutus* L. and *G. minutus* var. *microps* Kr. and *Gobius niger* L., 1.5 — 4.5 cm long from the bay and from the high sea were kept in aquariums containing water from the bay; the fishes were fed *Daphnia* sp. After a short period the fishes adapted themselves to the new conditions.

Table VI

Dimensions of cercariae of D.spathaceum (Rud.) in experimental invasion in microns

after:	20 h	28 h	2 days	3 days	6 days
Body	150 × 48	135-165 × 60	216 × 57	105-195	680-884 × 323
Ventral sucker	24	21	30 × 21	15 × 18	68
Anterior organ	45	39	36	24	-
Oral sucker					51
Holdfast organ					85 × 85

Then cercariae with the snail's liver as well as the whole snails *Radix ovata* var. *baltica* Nil. were put into the aquariums; there was one portion of the cercariae from one snail to every 4 fishes on the average. Attempts had been made at tracing back the transformations of the cercaria within the host's lense. For that purpose the fishes were dissected.

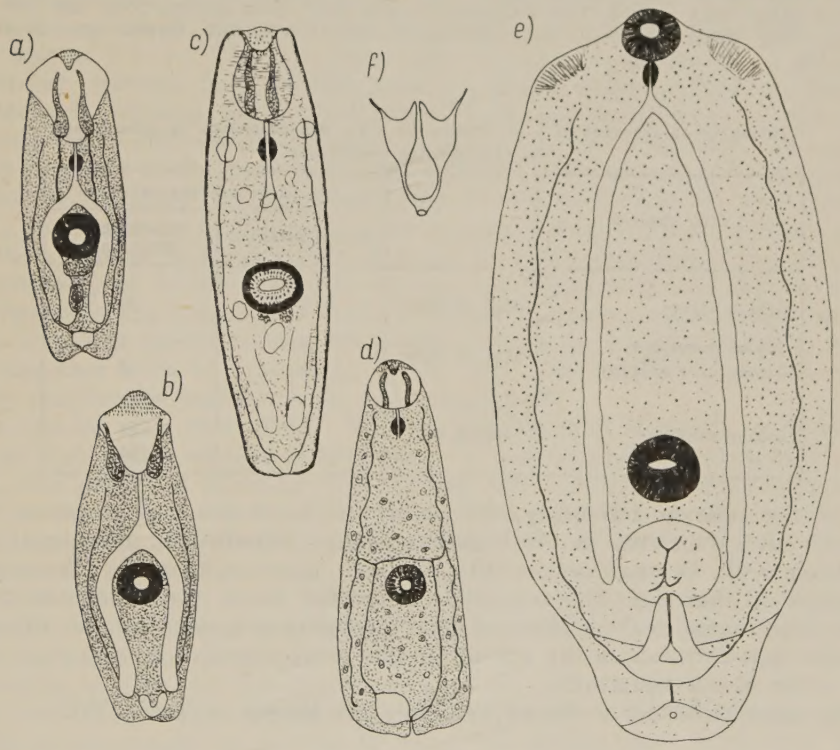


Fig. 5. The successive developmental forms of cercaria of *D. spathaceum* (Rud.) in the eye-lense of *Gobius minutus* L.: a — 20 hours, b — 28 hours, c — 2 days, d — 3 days, e — 6 days following infestation, f — form of the excretory vesicle

Fig. 5a shows a metacercaria 20 hours following infestation. While penetrating into the eye-lense, its body shrinked, the internal organs changed obviously, the penetration glands began to disappear their ducts becoming narrower, the excretory system changed too, and the body became gradually less transparent.

Fig. 5b represents a metacercaria 28 days following infestation. The four coarse-granular penetration glands had disappeared completly, and only their thickened ducts at the frontal part of the front organ remained, the whole body, opaque, is filled up with a granular substance.

The picture of the metacercaria two days following infestation is shown in Fig. 5c. The body seems a little shrunk, the intestinal ramifications almost unvisible. Two crowns of spines may already distincly appear on the ventral sucker. The excretory vesicle has slightly changed in shape.

Fig. 5d shows a metacercaria three days following infestation. The body became elongated and shrunk, the frontal organ has changed in shape gradually assuming

that of the future oral sucker; the intestine unvisible, except for the pharynx, the excretory ducts already appear quite distinctly, the excretory bladder assumed a new shape. The body became turbid.

A metacercaria 6 days following infestation is represented in Fig. 5e. Its dimensions and shape are those of the mature form. The body is not transparent at all, it is turbid, almost completely filled up with granular corpuscles. The excretory vesicle pulsates heavily changing in shape. The halves of the excretory vesicle swell up in their inferior part first, and extend frontally, as thin appendices and the other way round. The extretory ducts and their connections are not well visible. The dimensions of the successive developmental forms are given in Table VI.

Table VII

Intensity of invasion of D.spathaceum (R u d.) metacercariae in natural and in experimental conditions

Fish species		No. of metacercariae in	
		natural invasion	experimental invasion
Gobius niger	Gulf of Puck	6	20
Gobius minutus + G.minutus v.microps	Gulf of Puck	-	1
		6	9
Gobius minutus	Baltic Sea	-	10
		-	14
		-	20

For the sake of reliability, the observations on the matacercariae were carried out exclusively in the high sea *Gobius minutus* L., as natural lense infection with *D. spathaceum* (R u d.) was never noticed by the present authoress in that fish. The sea fishes supported worse the conditions of the experiment, some of them perished soon (probably as a result of the difference between salt contents in the sea water they normally live in and that in the bay water in the aquarium).

The data obtained in the experiments are shown in Table VII.

Discussion of results

The life-cycle of *Diplostomum spathaceum* (R u d.) studied in brackish conditions (both, natural and experimental) displayed some properties as were not confirmed in fresh water conditions.

1. The life-cycle was closed accurately within the range of the biocoenosis covering the biotope of the sand bottom thanks to the parasite wandering from the miracidium which came forth from the egg (in sea-gull's excrements), and which then, transforming itself, travelled from the snail into the fish and, finally, into the bird where it attained its mature form. The parasite's life-cycle could not be closed within other area in the bay as the absence of the proper hosts, *Radix ovata* var. *baltica* N i l s s., eliminated this parasite from the biocoenosis. Thanks to the same reason (the absence of hosts) the fishes in the inshore zone of the high sea were not invaded at all.

Thus, the spread of *D. spathaceum* (Rud.) is limited by the 1st host's occurrence in the biocoenosis.

2. In the environment examined, the cercaria exhibited considerable specificity towards *Radix ovata* var. *baltica* Nilss. as the latter proved to be the only appropriate host for this stage. Thus, the cercaria retained its fresh-water host, *Radix ovata,* belonging to fresh- water family *Lymnaeidae.* The metacercaria found other hosts, other than the fresh-water ones which (from the point of view of biocoenosis) were connected with *Radix ovata* var. *baltica* Nilss. The sea fishes such as: *Gobius minutus* L., *Gobius minutus* var. *microps* Kr., *Gobius niger* L., *Siphonostoma typhle* L., *Nerophis ophidion L.* became the proper hosts, while the fresh-water species *Esox lucius* L. and *Gasterosteus aculeatus* L. shifted to the background. The mature stage retained their fresh-water hosts. These are, according to the present authoress findings, the gulls belonging to the species *Larus ridibundus* L.

3. The intensity of invasion is considerably less in the conditions of the sea than in those of fresh water. Markevič 1951 established that the highest intensity of invasion of *Diplostomum spathaceum* (Rud.) was up to 500 specimens in the eyes of one fish. In present authoress experiment, the average intensity varied within the range from 6 to 15 metacercariae except for one case with 51 specimens in one fish. This could well be the result of the smaller dimensions of the fishes examined.

It can be seen from Table VII that the invasion intensity is, generally, not as high under natural conditions as it can be under experimental ones.

4. The period of duration of the complicated cercaria transformation into the metacercaria, carried out by the present authoress under experimental conditions, was considerably shorter than that confirmed by Szidat. As early as six days following infestation a metacercaria was obtained which equalled the mature form in dimensions in the experiment discussed; its body was already completely formed, although still almost opaque with many granular corpuscles and with a hardly visible secondary excretory system. According to Szidat, this shape was attained by the cercaria not earlier than two weeks following infestation. It could be admitted that this was the result of the environmental conditions in which the metacercaria could have transformed more quickly.

5. The morphological structure and dimensions of both, the cercaria and metacercaria as well as those of the mature forms were, generally, almost identical in the brackish and in the fresh water conditions.

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STRESZCZENIE

Autorka prześledziła przebieg cyklu rozwojowego *Diplostomum spathaceum* (Rudolphi 1819) w warunkach słonawych wód Zatoki Puckiej, przeprowadzając również uzupełniające próby eksperymentalnego zarażania ryb. Autorka stwierdza, że znany z wód słodkich cykl tej przywry może zamykać się w badanym środowisku jedynie w obecności w biocenozie błotniarki *Radix ovata* var. *baltica* Nilss., stanowiącej jedynego żywiciela sporocysty. Rolę żywiciela metacerkarii przejęły w Zatoce Puckiej przede wszystkim bardzo tu częste *Gobius minutus* L. i *G. minutus* var. *microps* Kr. Żywicielami postaci dojrzałej są mewy, przede wszystkim *Larus ridibundus* L. Autorka stwierdza zasadnicze podobieństwo obserwowanych przez siebie postaci rozwojowych *Diplostomum spathaceum* (Rud.) z Zatoki Puckiej z opisanymi z wód słodkich.